Dinoflagellate cysts as proxies of environmental, ocean and climate changes in the Atlantic realm during the quaternary

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Over the last four decades, organic-walled dinoflagellate cysts have shown high potential as tracers of past sea-surface conditions during the Quaternary. These microfossils relate to the pelagic productivity of both phototrophic and heterotrophic protist organisms and are recovered in high numbers in almost all marine environment settings from the nearshore and estuarine systems to the distal continental margin. In polar environments, where other conventional proxies are rare or absent, dinoflagellate cysts showed a relatively high diversity of species and a close relationship with sea-ice cover duration, winter and summer temperature, and salinity, enabling quantitative reconstructions of several oceanic variables over time. From the temperate to the tropical latitudes of the Atlantic Ocean, their modern distribution highlights a response to primary productivity and seasonal contrasts in surface temperature. They also have proven that they could be used as tracers of eutrophication in stratified systems and can also highlight human impact on their distribution. In this paper, we present an overview of dinoflagellate cysts as ecological tracers in recent and past sediments of the Atlantic Ocean, from the Arctic to the Antarctic. We provide examples of their use as proxies in paleoclimatic-palaeoceanographic studies at glacial to interglacial time scales, with emphasis on the last ice age to recent (last 25 kyr), the northern North Atlantic and western-eastern tropic North Atlantic. We also discuss their potential as tracers of anthropogenic stress in coastal environments.

1 Introduction

The phylum Dinoflagellata encompasses a large diversity of unicellular eukaryotic organisms, including phototrophic taxa, hence playing a major role in the biological pump (Falkowski, 2012). Dinoflagellates are currently found in all aquatic systems, mostly in marine waters, where at least 2377 species are known (Gómez, 2012a). They occur from high latitudes to the tropics and can be found even in sea ice (e.g., Mudie, 1992; Montresor et al., 2003). Some of them are known to create Harmful Algal Blooms (HABs) (i.e., *Alexandrium*, *Dinophysis*, *Karenia* species, etc.).

Dinoflagellates have a complex feeding strategy. Among them, several species are phototrophic and account for an important part of the primary productivity of the ocean together with haptophytes and diatoms (e.g., Sigman and Hain, 2012). However, about 58% of extant taxa are heterotrophic, and several are described as mixotrophs, symbionts or parasites (Gómez, 2012b). One of the striking features of this group is that about 20% of the species form cysts that protect hypnozygote during their life cycle and the cyst is made of highly resistant organic matter enabling preservation in the sediments (e.g., Head, 1996) (Figure 1). These cysts are recovered in palynological slides after chemical treatments involving hydrochloric and hydrofluoric acids, and they are commonly analysed by palynologists as other organic-resistant microfossils such as pollen and spores (Traverse, 1974).

Close to a hundred organic-walled dinoflagellate cyst (also called dinocyst) taxa have been described from recent sediments (Van Nieuwenhove et al., 2020a; Limoges et al., 2020; Mertens et al., 2020). In addition, 35 known extant marine taxa make a calcareous cyst that can also be found in marine sediments (Zonneveld et al., 2005).

Dinoflagellate cysts have been observed in sedimentary rocks dating since the Triassic and used with success as biostratigraphic markers in Mesozoic and Cenozoic sequences (e.g., Fensome et al., 1993). In the 1970s, their significance as a palaeoceanographical indicator emerged with the pioneering studies of Williams (1971), Davey and Rogers (1975), Wall et al. (1977) and Williams and Bujak (1977) dealing with deep-sea sediment of the Atlantic Ocean. Earlier on, the ground-breaking studies of Braarud (1945) and later on of Nordii (1951), Wall (1965) and Wall and Dale (1966) elucidated the relationship between the motile form found in surface waters and the cyst, settled in the sediments, helping to understand the ecological affinities of these organisms. Since then, numerous studies focused both on culture and rDNA sequencing have further increased our knowledge of this relationship (e.g., Wang et al., 2019; Gu et al., 2021, 2022), clarifying taxonomical conundrums.

In the last thirty years, the use of dinoflagellate cyst assemblages in palaeoecology and palaeoclimatology increased considerably, notably with the development of approaches allowing quantitative estimates of past climate and ocean parameters. Here, we present the state of the knowledge concerning dinoflagellate cysts and their
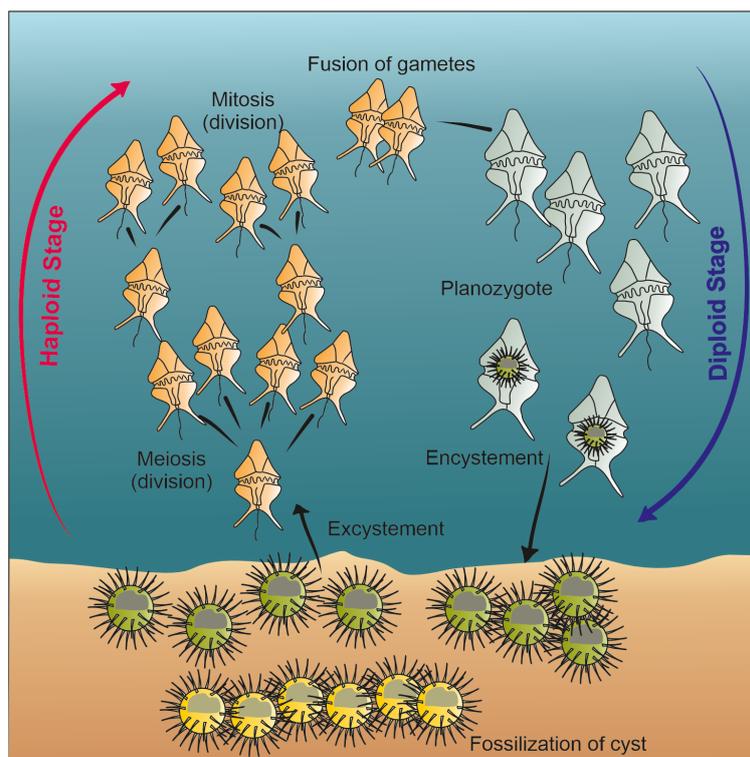

FIGURE 1
Simplified schematic of dinoflagellate life cycle, modified after de Vernal et al. (2013c) and Bravo and Figueroa (2014).

TABLE 1 List of organic-walled dinoflagellate cyst species found worldwide, with motile stage and trophic status (T is for Trophic habit, with P including phototrophs and autotrophs, H for heterotrophs and M for mixotrophs.

T	Cyst name (with code)	Thecate equivalent	Arc	SubA	TempNA	Intertrop	TempSA	AAO	PacO	IndO
P	*Achomosphaera andalousiense* (Aand)	*Gonyaulax* sp.	■	■	■					
P	*Ataxiodinium choane* (Atax)	*Gonyaulax spinifera*		■	■					
P	*Bitectatodinium spongium* (Bspo)	Unknown			■	■	■		■	■
P	*Bitectatodinium tepikiense* (Btep)	*Gonyaulax digitale*	■	■	■			■		
P	*Dalella chathamense* (Dcha)	Unknown	■	■	■	■		■		
P+	Cyst of *Gymnodinium* spp. (Gymn)	**Gymnodinium spp.**				■				
P	*Impagidinium aculeatum* (Iacu)	Unknown	■	■		■	■	■	■	■
P	*Impagidinium japonicum* (Ijap)	Unknown		■	■	■	■	■	■	
P	*Impagidinium pallidum* (Ipal)	Unknown	■	■			■	■	■	■
P	*Impagidinium paradoxum* (Ipar)	Unknown			■	■	■	■	■	■
P	*Impagidinium patulum* (Ipat)	Unknown			■	■	■	■	■	■
P	*Impagidinium plicatum* (Ipli)	Unknown	■	■	■			■		
P	*Impagidinium sphaericum* (Isph)	Unknown	■	■	■			■	■	■
P	*Impagidinium strialatum* (Istr)	Unknown			■	■	■	■	■	■
P	*Impagidinium variaseptum* (Ivar)	*Gonyaulax bohaiensis*			■			■	■	■
P	*Impagidinium velorum* (Ivel)	Unknown				■			■	
P	*Nematosphaeropsis labyrinthus* (Nlab)	Unknown	■	■	■	■	■	■	■	■
P	*Nematosphaeropsis rigida* (Nrig)	Unknown		■			■		■	
P	*Operculodinium aguinawense* (Oagu)	Unknown				■			■	■
P	*Operculodinium centrocarpum* sensu Wall and Dale, 1966 (Ocen)	**Protoceratium reticulatum**	■	■	■	■	■	■	■	■
P	*Operculodinium giganteum* (Ogig)	Unknown			■	■	■		■	■
P	*Operculodinium israelianum* (Oisr)	Unknown			■	■	■	■	■	■
P	*Operculodinium janduchenei* (Ojan)	Unknown		■					■	■
P	*Operculodinium longispinigerum* (Olon)	Unknown			■	■	■	■	■	
P	Cyst of *Pentapharsodinium dalei* (Pdal)	*Pentapharsodinium dalei*	■	■	■			■	■	■
P	Cyst of *Polarella glacialis* (Pgla)	*Polarella glacialis*	■					■		
P	*Polysphaeridium zoharyi* (Pzoh)	**Pyrodinium bahamense**			■	■	■	■	■	■
P	*Pyxidinopsis reticulata* (Pret)	Unknown		■	■		■			
P	*Pyxidinopsis psilata* (Ppsi)	Unknown		■			■	■		
P	*Spiniferites belerius* (Sbel)	*Gonyaulax scrippsae*		■	■	■	■			
P	*Spiniferites bentorii* (Sben)	*Gonyaulax nezaniae*		■	■	■	■		■	■
P	*Spiniferites bulloideus* (Sbul)	*Gonyaulax* sp.	■	■	■	■	■		■	■
P	*Spiniferites delicatus* (Sdel)	*Gonyaulax* sp.		■	■	■	■		■	■
P	*Spiniferites elongatus* (including *Spiniferites frigidus* and *Rottnestia amphicavata*) (Selo)	*Gonyaulax ovum* comb. nov.	■	■	■	■	■	■	■	■
P	*Spiniferites lazus* (Slaz)	Unknown		■	■		■		■	
P	*Spiniferites membranaceus* (Smem)	*Gonyaulax lewisiae* sp. nov.		■	■	■	■	■		■
P	*Spiniferites mirabilis* (includes *S. hyperacanthus*) (Smir)	*Gonyaulax spinifera*		■	■	■	■	■	■	■
P	*Spiniferites pachydermus* (Spac)	*Gonyaulax ellegaardiae*		■	■	■	■	■	■	■

(Continued)

TABLE 1 Continued

T	Cyst name (with code)	Thecate equivalent	Arc	SubA	TempNA	Intertrop	TempSA	AAO	PacO	IndO
P	*Spiniferites ramosus* (Sram)	*Gonyaulax spinifera*	■	■	■	■	■	■	■	
P	*Spiniferites* sp. granular type (Sgra)	Unknown	■	■	■	■	■	■	■	
P	*Spiniferites* spp. (Sspp)	Unknown	■	■	■	■	■	■	■	■
P	*Tectatodinium pellitum* (Tpel)	*Gonyaulax spinifera*	■	■	■			■	■	■
P	*Tuberculodinium vancampoae* (Tvan)	*Pyrophacus steinii*						■		
M	*Lingulodinium machaerophorum* (Lmac)	**Lingulodinium polyedra**	■	■	■	■	■	■	■	■
H	*Brigantedinium* spp. (Bspp)	*Protoperidinium* spp.	■	■	■	■	■	■	■	■
H	*Cryodinium meridianum* (Cmer)	Unknown	■	■	■	■	■	■		
H	Cyst of *Polykrikos* sp. arctic morphotype (Parc)	*Polykrikos* sp.	■	■	■				■	
H	*Dubridinium* spp. (Dubr)	*Preperidinium* sp.	■	■	■	■	■	■	■	
H	*Echinidinium aculeatum* (Eacu)	Unknown	■	■	■	■		■	■	
H	*Echinidinium bispiniformum* (Ebis)	Unknown		■	■		■		■	■
H	*Echinidinium delicatum* (Edel)	Unknown	■	■	■	■		■	■	
H	*Echinidinium granulatum* (Egra)	Unknown			■	■	■	■	■	
H	*Echinidinium karaense* (Ekar)	Unknown	■	■	■			■	■	■
H	*Echinidinium* spp. (Espp)	Unknown	■	■	■	■	■	■	■	■
H	*Echinidinium transparantum* (Etra)	Unknown			■	■	■	■	■	
H	*Islandinium brevispinosum* (Ibre)	*Protoperidinium haizhouense*		■	■	■			■	
H	*Islandinium cezare* (Imic)	Unknown	■	■					■■	
H	*Islandinium minutum* (Imin)	*Islandinium minutum*	■	■	■			■	■	
H	*Lejeunecysta* spp. (Lspp)	*Protoperidinium* spp.		■	■	■	■		■	■
H	*Nucicla umbiliphora* (Numb)	Unknown						■		
H	Peridinoids (Peri)	Unknown	■	■	■	■	■	■	■	■
H	*Peridinium ponticum* (Ppon)	*Protoperidinium* spp.		■				■■		
H	Cyst of *Polykrikos kofoidii* (Pkof)	*Polykrikos kofoidii*	■	■	■	■	■	■	■	
H	Cyst of *Polykrikos schwartzii* (Psch)	*Polykrikos schwartzii*	■	■	■	■	■	■	■	
H	Cyst of *Protoperidinium americanum* (Pame)	*Protoperidinium americanum*	■	■	■			■	■	
H	Cyst of *Protoperidium minutum* (Pmin)	*Protoperidinium minutum*	■	■		■	■		■	
H	Cyst of *Protoperidinium monospinum* (Pmon)	*Protoperidinium monospinum*				■		■		
H	Cyst of *Protoperidinium nudum* (Pnud)	*Protoperidinium nudum*		■	■	■	■	■	■	
H	Cyst of *Protoperidinium stellatum* (Pstel)	*Protoperidinium stellatum*		■	■	■	■	■	■	
H	*Quinquecuspis concreta* (Qcon)	*Protoperidinium leonis*	■	■	■			■	■	
H	*Selenopemphix antarctica* (Sant)	Unknown		■			■	■	■	
H	*Selenopemphix nephroides* (Snep)	*Protoperidinium subinerme*		■	■	■	■	■	■	
H	*Selenopemphix quanta* (Squa)	*Protoperidinium conicum*	■	■	■	■	■	■■	■	
H	*Stelladinium bifurcatum* (Sbif)	Unknown		■		■	■		■	
H	*Stelladinium reidii* (Srei)	Unknown								■
H	*Stelladinium robustum* (Srob)	Unknown								■

(Continued)

TABLE 1 Continued

T	Cyst name (with code)	Thecate equivalent	Arc	SubA	TempNA	Intertrop	TempSA	AAO	PacO	IndO
H	*Trinovantedinium applanatum* (Tapp)	*Protoperidinium shanghaiense*		▓	▓	▓	▓		▓	
H	*Trinovantedinium pallidifulvum* (Tpal)	*Protoperidinium louisianensis*		▓	▓					
H	*Trinovantedinium variabile* (Tvar)	Unknown							▓	
H	*Votadinium calvum* (Vcal)	*Protoperidinium oblongum*	▓	▓	▓					
H	*Votadinium spinosum* (Vspi)	*Protoperidinium claudicans*		▓	▓		▓			
H	*Xandarodinium xanthum* (Xxan)	*Protoperidinium divaricatum*		▓		▓				
?	*Melitasphaeridium choanophorum* (Mcho)	Unknown								

P+ includes species known to be phagotrophic) (data compiled from Marret et al. (2020) and other studies cited in Table 2). Thecate species in bold are known for producing toxins. Shaded grey indicates where the species has been identified in the Arctic (I), Subarctic (II), Temperate North Atlantic Ocean (III), Intertropical Atlantic Ocean (IV), Temperate South Atlantic Ocean (V), Antarctic Atlantic Ocean (VI), Pacific Ocean (VII), Indian Ocean (VIII)- Cells with dark shade indicate the possible identification of the species but not confirmed.

ecology, we provide some insight into the use of assemblages to document palaeoceanographical changes in the Atlantic Ocean during cold and warm episodes of the late Quaternary, and we briefly outline some environmental issues involving dinoflagellates and their cysts. Furthermore, this review integrates up-to-date considerations on the distribution of dinocysts both in time (biostratigraphy and ecostratigraphy) and space, from the high latitudes of the Northern Hemisphere to the Southern Ocean, following a major update of the taxonomy (Van Nieuwenhove et al., 2020b).

2 General characteristics of dinoflagellate cysts as a palaeoecological indicator from sediment studies

The life cycle of dinoflagellate is complex, with a hiatus between the thecal stage of living populations and the cyst stage, related to sexual reproduction, that fossilises in the sediment. Whereas thousands of living species are known, less than a hundred recent dinoflagellate cyst taxa were described. Hence, the cyst record only provides a fragmentary picture of the original populations. Furthermore, the morphology of the cyst is distinct from that of the theca, which makes cyst identification one of the most challenging aspects of the analysis. This is particularly critical for some taxa that exhibit a large range of morphological variability. The *Spiniferites* species are a typical example with shapes showing large variations (e.g., de Vernal et al., 2018; Mudie et al., 2018; Gu et al., 2021). The cyst morphology is the basis for the identification. The shape and the tabulation of the cyst body, the shape and position of the archeopyle, the ornamentation, processes density, shape and position, the wall structure, and sometimes the colour of the wall are all typical characteristics used to identify species.

Several comprehensive atlases have been produced over the last decades, illustrating most of the modern dinoflagellate cyst species (e.g., Rochon et al., 1999; Zonneveld et al., 2013; Zonneveld and Pospelova, 2015; Mudie et al., 2017; Limoges et al., 2018, 2020; Mertens et al., 2020; Van Nieuwenhove et al., 2020a).

Another layer of complexity in the study of fossil dinoflagellate cysts is related to the dual terminology used to identify dinoflagellates and their cysts that are observed in distinct types of samples (it follows the *International Code for the Nomenclature of Algae, Fungi and Plants* (the Shenzhen Code, Turland et al., 2018). On the one hand, we have biological names for the thecate stage, and on the other hand, we have micropalaeontological names for the cyst stage yielding fossils (see Head, 1996; Ellegaard et al., 2018; Head et al., 2024). Although it has not been officially agreed, in general, studies dealing with cysts use the micropalaeontological name, unless the cyst was originally described from specimens of known biological affinity (see Table 1).

The wall of organic-walled dinoflagellate cysts is made of a strong molecules, often called dinosporin although recent studies have shown complex compositions depending upon the taxa. Studies based on micro-Fourier-transformed infrared spectroscopy have highlighted distinct compositions whether the taxon is phototrophic (cellulose-like glucan) or heterotrophic (nitrogen-rich glucan) (e.g., Bogus et al., 2014; Gurdebeke et al., 2018, 2020; Meyvisch et al., 2022, 2023). Some studies on the preservation aspect of organic matter in oxic and anoxic environments have tentatively established a classification of taxa according to a sensitivity gradient, with most phototrophic species being relatively resistant whereas heterotrophic species would be more prone to early diagenetic processes (e.g., Zonneveld et al., 2008, 2019; Versteegh and Zonneveld, 2022).

The complexity of the life cycle of dinoflagellates and the fact that the production of cysts is still not fully understood, as most of the observations are based on controlled conditions in laboratories (e.g., Bravo and Figueroa, 2014), has long been a limitation in

palaeoecology. Consequently, the establishment of dinoflagellate cysts as a palaeoecological indicator slowly evolved, and from studies on the distribution of these microfossils in recent sediments (e.g., Wall et al., 1977; Williams and Bujak, 1977; Harland, 1983; Turon, 1984; Rochon et al., 1999). Mapping their occurrence in the oceans and relating their relative abundance with surface conditions was the stepping-stone to enable this microfossil group to become a valuable tracer of sea-surface conditions (e.g., Rochon et al., 1999; de Vernal et al., 2001; Marret and Zonneveld, 2003; Zonneveld et al., 2013; de Vernal et al., 2020).

Overall, the increasing number of studies investigating the distribution of dinoflagellate cyst species in recent sediments (Figure 2) has greatly contributed to refining our knowledge of their ecological affinity, sometimes shifting paradigms for some species. In parallel, progress in culture techniques and genetic studies has enabled to clarification of the idea that some thecate species may "create" different cyst species likely related to environmental conditions (the *Spinifera* complex, e.g., Ellegaard et al., 2018). Although there are taxonomical uncertainties and despite the hiatus between living and fossil populations, dinoflagellate cysts are now considered very useful palaeoceanographical tracers in marine environments of continental margins.

3 Modern distribution of dinoflagellate cysts

Until the 1970s, most studies dealing with fossil dinoflagellate cysts, then designated as hystrichospheres, were undertaken by sedimentary geologists to document the Mesozoic-Cenozoic biostratigraphy. The demonstration of the relationships between dinoflagellates and their cysts based on detailed morphological observations of fossils (Evitt, 1963), observation of

hystrichospheres in the plankton (Wall, 1965) and culture experiments (Wall and Dale, 1966, 1968) were an important step toward the use of dinoflagellate cysts in palaeoecology. Based on dinoflagellate cyst taxa counts in 35 surface sediment samples from the North Atlantic Ocean, Williams (1971) demonstrated a distribution related to environmental gradients, from nearshore to offshore settings and with latitudes. Later, Wall et al. (1977) made a comprehensive analysis of the distribution of dinoflagellate cysts in sediments collected at 168 sites from tropical to temperate latitudes of the Atlantic Ocean showing further distinct associations related to the latitudinal gradients, in addition to assemblages having affinities for either estuarine, neritic or oceanic environments. Hence, they proposed an ecological classification of taxa in categories and associations, which could be used as a conceptual model for the understanding of taxa distribution (Figure 3).

Since the early works of Williams (1971) and Wall et al. (1977), regional studies permitted to develop distribution maps of dinoflagellate cysts in sediments of the North Atlantic and adjacent seas (e.g., Harland, 1983; Turon, 1984; de Vernal et al., 1994; Rochon et al., 1999), the Northern Hemisphere Oceans (Radi and de Vernal, 2008; de Vernal et al., 2013a, 2020) and at World Ocean scale (Marret and Zonneveld, 2003; Zonneveld et al., 2013; Marret et al., 2020; see Figure 2). Hence, much progress in the knowledge of the distribution of dinoflagellate cysts in surface sediments has been made in the last decades, strengthening the early observation and inferences by Wall et al. (1977).

Dinoflagellate cysts recovered in sediment are related to pelagic productivity but the taphonomic processes between the dinoflagellate population in upper water mass and their cysts in the thanatocoenoses have been a matter of debate. Comparison of dinoflagellate in plankton tows (theca) and sediment traps or sediments at the sea floor (cysts) have shown a general agreement in the taxonomic content allowing inferences about dinoflagellate populations in surface water and cyst assemblages in the sediment
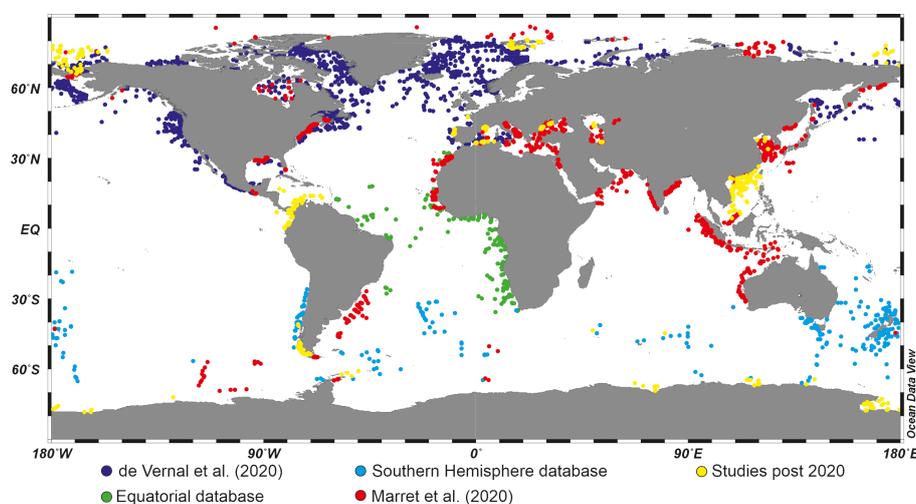

FIGURE 2
Global distribution of organic-walled dinoflagellate cyst assemblages in surface sediments, based on a compilation from Marret et al. (2020) with additional studies published post 2020 (see Table 2 for references).

TABLE 2 Location of datasets used in Figure 2 here with references.

Datasets	References	Number of sites
DB=1968	de Vernal et al. (2020)	1968
Equatorial Database	Marret et al. (2020)	202
Southern Hemisphere Database	Marret et al. (2020)	310
Other sites in Marret et al. (2020)	Marret et al. (2020)	1216
Chukchi Sea – Eastern region	Kim et al. (2023)	32
Chukchi Sea – Western region	Obrezkova et al. (2023)	22
Svalbard fjords	Telesiński et al. (2023)	25
Southern Brittany, Atlantic Ocean	Lambert et al. (2022)	15
Ria de Vigo, Atlantic Ocean	García-Moreiras et al. (2023)	82
Patagonia, Chile	Salgado et al. (2023)	31
Mediterranean Sea	Coussin et al. (2022)	24
Caspian and Black Seas	Sala-Pérez et al. (2020)	36
Black and Marmara Seas	Mudie et al. (2021)	43
Southern Caribbean	Ramírez-Valencia et al. (2021)	24
Eastern Tropical Pacific Ocean	Ramírez-Valencia et al. (2021)	28
South China Sea	Li et al (Li et al., 2020, 2023)	82
Southern Ocean	Thöle et al. (2023)	60

Datasets with asterisk were published post Marret et al. (2020).

FIGURE 3
Schematic distribution of some taxa according to general ecosystems and stress vectors determined by estuarine-neritic to offshore gradients (salinity, turbulence, water depths, nutrients) and tropical to polar latitudes (temperature, seasonal contrasts). The sketch with the categories of dinocyst taxa having affinities for neritic, estuarine and offshore settings in tropical to cool temperate environment was inspired by Wall et al. (1977). Only a few taxa are indicated in the figure, most being categorized by Wall et al. (1977). The cosmopolitan taxa *Brigantedinium* spp., *Operculodinium centrocarpum* and *Nematosphaeropsis labyrinthus* are not shown.

(e.g., Dodge and Harland, 1991; Dodge, 1994; Heikkilä et al., 2016) although only a small proportion of dinoflagellate taxa produces fossilisable cysts (e.g., Head, 1996). While a large part of the cyst fluxes is likely to derive from the upper water masses through settling with marine snow and faecal pellets (Turner, 2015), hydrodynamic factors can be involved in the sedimentation of the cysts (Wall et al., 1977; Nooteboom et al., 2020). Hence, lateral transport of dinoflagellate cysts before burial as any other small-size particles cannot be ruled out. Nevertheless, the sharp boundaries in the cyst distribution on the sea floor suggest a limited impact of distal transport on the assemblages (e.g., de Vernal et al., 2020), as also shown at the zonal scale through modelling experiment (Thöle et al., 2023). The analyses of other microfossils recovered in palynological slides such as pollen and spores that are necessarily allochthonous provide clues about potential nearshore-offshore transport, which appears very limited beyond the estuarine and inner neritic zone (e.g., de Vernal and Giroux, 1991; Rochon and de Vernal, 1994). Among taphonomical processes, selective
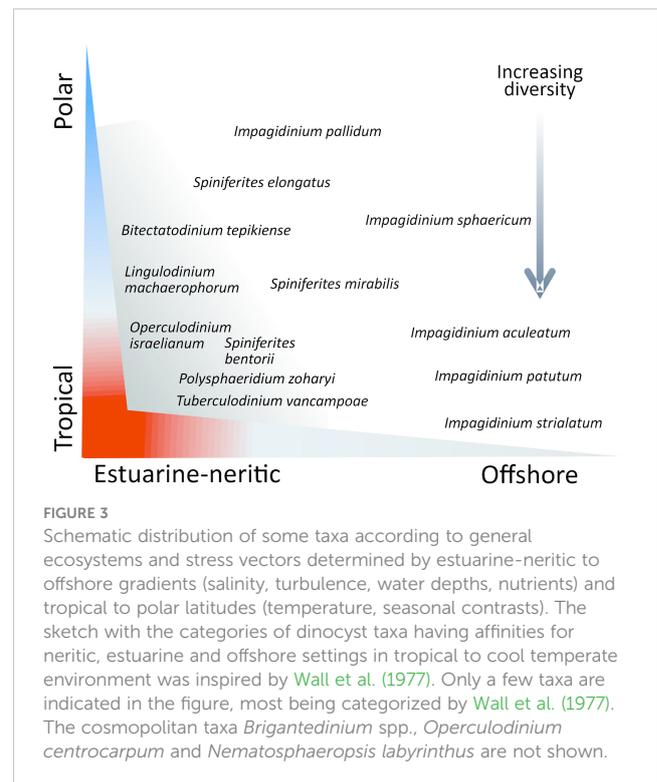
preservation could be considered. It has been shown that the organic-walled cysts of some taxa, notably those belonging to protoperidinales, could be affected by oxidation (Zonneveld et al., 2008, 2019). Nevertheless, despite possible biases due to differential preservation, the analysis of cyst distribution in recent sediments highlights close relationships with sea-surface conditions (e.g., de Vernal et al., 2020). Abundant protoperidiniale cysts recovered in the sediment may also suggest a limited impact of oxidation, at least along continental margins where productivity is high and sedimentary inputs result in rapid burial.

In general, the concentrations of organic-walled dinoflagellate cysts are high in neritic marine environments and decrease offshore, showing very little fluxes in the distal deep ocean settings (Figure 4A). Such a feature may be due to generally low dinoflagellate productivity in central parts of the ocean, but also to poor preservation or both. Hence, dinoflagellate cysts appear particularly useful for the study of continental margin areas, where their species diversity and abundance are high (Figure 4B).

The modern distribution of dinoflagellate cysts around the world documents the geographical range and ecological affinities of the species. Many taxa can be considered cosmopolitan, meaning they occur in most of the oceans and seas, while others have a more restricted spatial distribution (e.g., Marret et al., 2020). Table 1 highlights that most taxa are found in the three oceans, but their relative abundance can vary in importance. Among the 83 taxa that we discuss here, very few are strictly endemic, and these are mostly found in the Southern Ocean, close to the Antarctic continent (Figure 5). Although McMinn (1995) initially reported the absence of Quaternary dinoflagellate cysts south of 60°S, subsequent studies
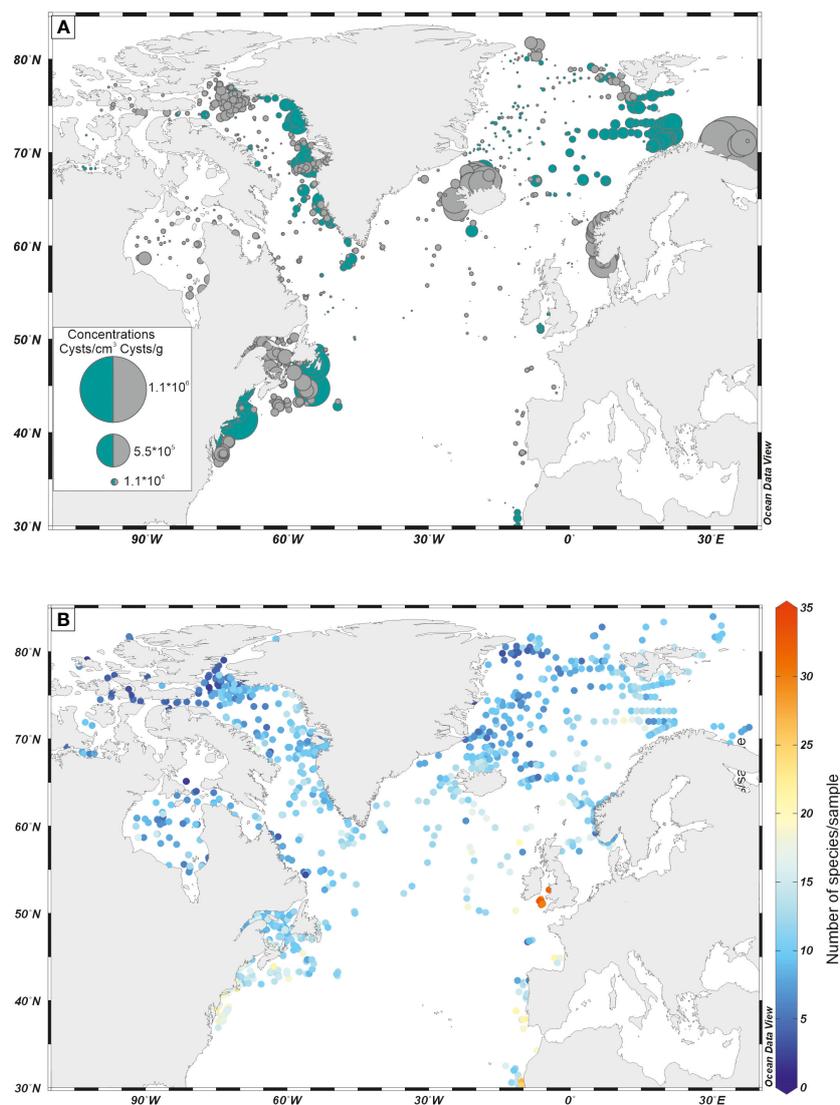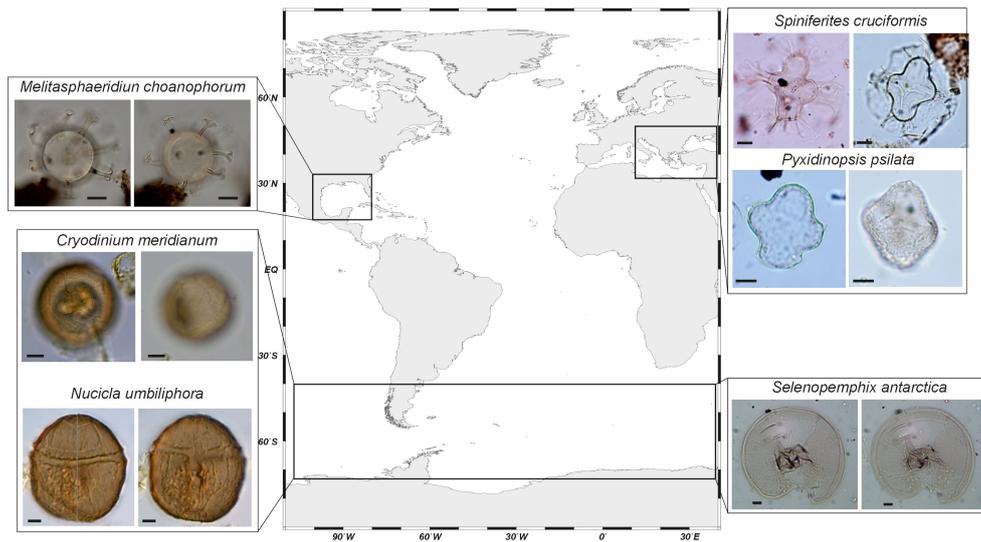
FIGURE 4
(A) Distribution map of cyst concentration (in specimen/g and specimen/cm³) in surface samples, in the North Atlantic Ocean; **(B)** Number of species per assemblage in surface samples, in the North Atlantic Ocean. Dinoflagellate cyst data are from the database DB=1968 (de Vernal et al., 2020).

highlighted a relatively the occurrence of up to 15 taxa, including the new species *Cryodinium meridianum*, *Nucicla umbiliphora*, and *Selenopemphix antarctica* (Marret and de Vernal, 1997; Esper and Zonneveld, 2002; Hartman et al., 2019). Another spot of endemism well documented is the Black Sea-Caspian Sea region, with some species being a legacy from the Paratethyan Sea (e.g., Mudie et al., 2018). It can be noted that recent human activities have enabled the spread of some endemic species. One example is that of *Peridinium ponticum*, an endemic species from the Ponto-Caspian region abundant in the northwestern part of the Black Sea (Mudie et al., 2017), but recently reported to occur in the Ria de Vigo (Atlantic margin of NW Iberia; García-Moreiras et al., 2023) and off Brittany (Mudie et al., 2017). In these cases, ballast waters, which are rich in micro-organisms that can relocate and thrive in different geographical regions (e.g., Cheniti et al., 2018), may have constituted an efficient mechanism for cyst dispersal.

4 From biostratigraphy to quantitative palaeoceanography in the Northern Hemisphere

4.1 Biostratigraphy, ecostratigraphy and climate changes

At the scale of the Mesozoic and Cenozoic, dinoflagellate cysts were used as biostratigraphy markers, and their distribution revealed maximum taxonomic diversity during the Cretaceous and Palaeogene (Fensome et al., 1993, 2019; Riding et al., 2022). Hence, dinoflagellates, or at least the taxa yielding organic-walled cysts, show affinities with warm oceans. During the Neogene, since about 23 Ma, a decreasing diversity of species appears to be a common feature in many time series (e.g., Wrenn and Kokinos, 1986; Head and Wrenn, 1992). It seems to have been accompanied by a decrease in the proportion of
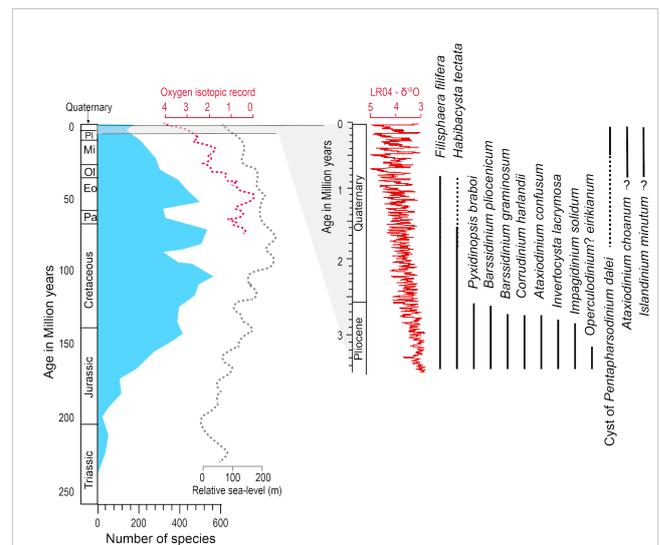
FIGURE 5
Endemism in dinoflagellate cyst population. Photos from *Spiniferites cruciformis* and *Pyxidinopsis psilata* are from the Holocene of the Black Sea (core MAR02−45P, Marret et al., 2009; photos are from courtesy of Fabienne Marret). Photos of *Selenopemphix antarctica* are from the Holocene off Adélie Land (core MD03−2601, photos are from courtesy of Fabienne Marret). Photos of *Melitasphaeridium choanophorum* are from the Cariaco Basin, ODP Site 1002, core section 1H 5W 11−13, courtesy of Kenneth Mertens). Photos of *Cryodinium meridianum* and *Nucicla umbiliphora* from recent sediments off Antarctica are courtesy of Julian Hartman and Francesca Sangiorgi (Hartman et al., 2018, 2019). Scale bar is 10μm.

warm water relative to cold water taxa and was thus associated with a global cooling trend (Boyd et al., 2018). From the early Pliocene to the Quaternary (5.33–2.58 Ma), which is an interval marked by the development of ice sheets in the Northern Hemisphere, the decrease in species diversity of dinoflagellate cysts continued with many disappearances and rare new occurrences of new taxa. This has been documented from several drilling sites in the northern North Atlantic (e.g., De Schepper and Head, 2008, 2009; De Schepper et al., 2017; Aubry et al., 2020), where assemblage changes could result from ocean re-organisation linked to global cooling, sea-level variations and Arctic gateway configuration changes at the onset of glaciations (e.g., De Schepper et al., 2015). A relationship between dinocyst biodiversity and global climate thus emerges from biostratigraphical schemes of the Cenozoic (De Schepper et al., 2015; Boyd et al., 2018). However, the timing of the biostratigraphic events and their distribution in space is not documented well enough to elucidate the mechanisms. In addition to the large-scale climate changes involving temperature shifts, the sea-level variations and the rapid modification of the physiography and coastlines during the glaciations and the transitions from glacial to interglacial stages might have represented major stresses for cyst-forming dinoflagellates. In particular, the emergence of shelves and ice advances over the continental margins might have been critical for the taxa with a life cycle involving a benthic stage before germination, and cell migration to the upper water column.

The few biostratigraphic schemes available for the Quaternary period suggest little turnover of dinoflagellate cyst taxa. However, the last occurrences of a few taxa including *Habibacysta tectata* and *Filisphaera filifera*, which progressively disappeared from the Arctic Ocean and the northern North Atlantic over the last two million years (de Vernal et al., 1992; Matthiessen et al., 2018; Figure 6), seems to correspond to the intensification of glaciations (Lisiecki

and Raymo, 2005) and possibly the development of perennial sea-ice cover in the Arctic Ocean (Polyak et al., 2013). Conversely, some taxa such as the cyst of *Pentapharsodinium dalei* recorded their first occurrence and increase in abundance at high latitudes during the

FIGURE 6
Figure illustrating the taxonomic diversity of dinoflagellate cyst though time. At the scale of the Mesozoic and Cenozoic, the figure is redrafted from Sluijs et al. (2005), with the number of species being from MacRae et al. (1996) and sea level curve from Haq et al. (1987). The Oxygen isotopic curve of the Cenozoic and the last 3.5 million years are from Cramer et al. (2009) and Lisiecki and Raymo (2005), respectively. At the scale of the latest Pliocene and Quaternary, the biostratigraphic ranges of a few species typical of the northern North Atlantic is illustrated from de Vernal et al. (1992), De Schepper et al. (2017) and Aubry et al. (2020).

Quaternary (Figures 6, 7), which could also relate to a global cooling trend.

At the scale of the Quaternary, marked by the alternation of glacial and interglacial stages, with global sea-level changes ranging up to 140 meters (Lisiecki and Raymo, 2005; Lambeck et al., 2014; Dutton et al., 2015), dinoflagellate cysts were used as ecostratigraphic markers. A few studies from the Northern North Atlantic document changes over several glacial to interglacial cycles (de Vernal and Mudie, 1992; Eynaud, 1999). Among those, the analysis of an 800,000-year long sequence at the Ocean Drilling Site (ODP) 646 in the northwest North Atlantic (Figure 7), shows large variations following the pacing of glacial-interglacial cycles. High concentrations, thus cyst fluxes, characterized the interglacial stages while changes in assemblages point to variations of temperatures from cool to temperate.
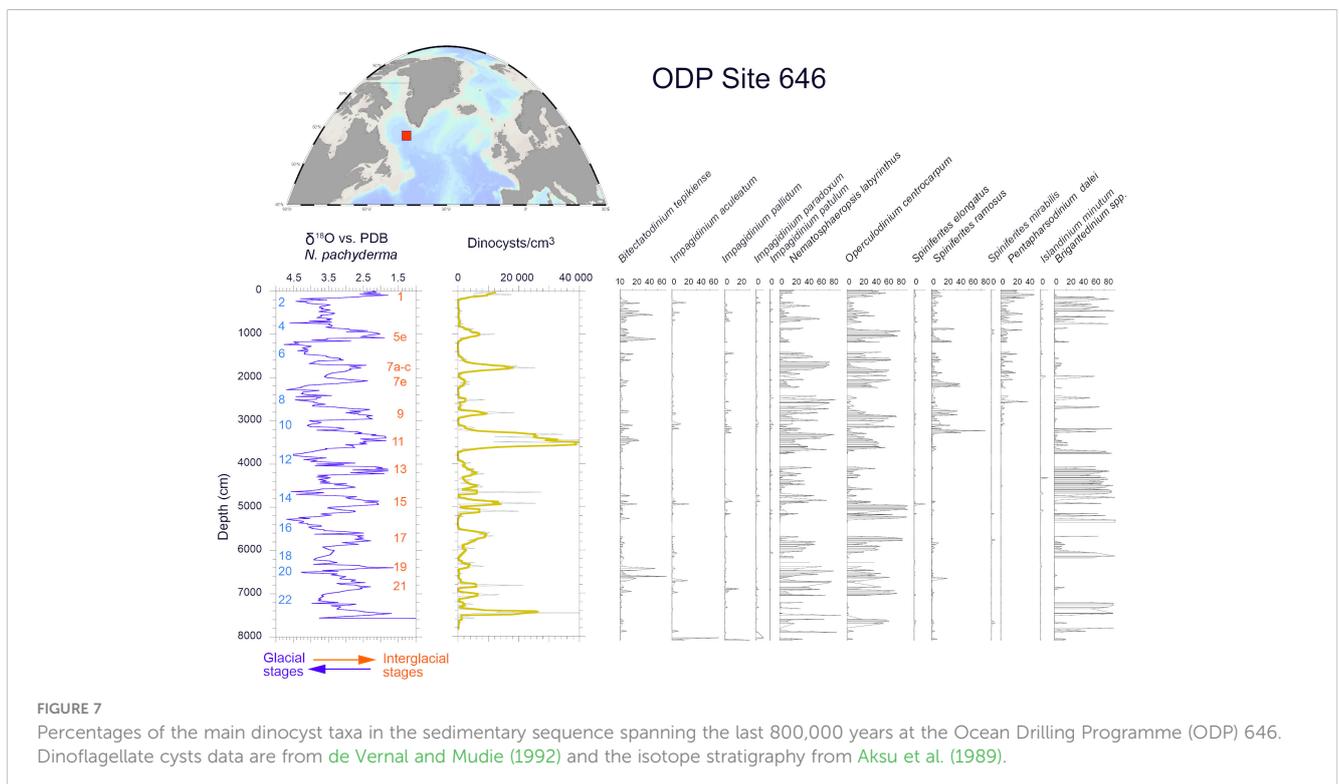
Among phototrophic taxa, the cosmopolitan species *Nematosphaeropsis labyrinthus* and *Operculodinium centrocarpum* are abundant and the accompanying taxa having affinities for more distinct environments illustrate important changes. For example, *Spiniferites mirabilis*, a taxon presently characteristic of warm temperate conditions (Figure 8A, de Vernal et al., 2018), recorded a small peak at ODP Site 646 during the last interglacial (marine isotope stage -MIS- 5e). It recorded maximum occurrences in MIS 5e sediments of several sites of the northern North Atlantic and Nordic Seas (Penaud et al., 2008), pointing to the spreading of warm temperate waters in the northern North Atlantic (Figure 8B). Another example is provided by the distribution of *Bitectatodinium tepikiense*, which presently characterizes the margin of southeastern Canada where low sea-surface salinity results in strong stratification, low thermal inertia and large contrasts of temperatures from freezing winters to warm

summers (de Vernal et al., 2005, 2020; Figure 9A). This taxon invaded the North Atlantic episodically, indicating episodes of large meltwater-freshwater discharges, notably during the last ice age (cf. de Vernal et al., 2005; Figure 9B).

In general, phototrophic taxa appear dominant during interglacial stages while heterotrophic taxa often characterize glacial intervals. In the northern North Atlantic, the dominance of heterotrophic taxa is common along continental margins marked by sea ice spreading during glacial times (Figure 10A). A high proportion of heterotrophic taxa, low species diversity, and common occurrence of *Islandinium minutum* (Figure 10B) are typical features of seasonal sea ice environments (de Vernal et al., 2001, 2013b, 2020). This could be related to primary productivity dominated by diatoms, which have the particularity to make blooms at the sea-ice edges, thus being more competitive than phototrophic dinoflagellates but providing food for heterotrophic taxa (e.g. Hamel et al., 2002; Radi and de Vernal, 2008).

4.2 Quantifying ocean changes from dinoflagellate cyst assemblages

Quantitative interpretations using transfer functions or analogue methods require standardised databases. The uniformization of the laboratory procedures and dinoflagellate cyst taxonomy undertaken permitted the development of a modern database of the Northern Hemisphere that was regularly updated since the 1990s (de Vernal et al., 1994; Rochon et al., 1999; de Vernal et al., 2001, 2013a, 2020). The last update includes 1968 sites and 71 taxa (de Vernal et al., 2020; Van Nieuvenhowe et al., 2020b). Before making reconstructions, it was necessary to
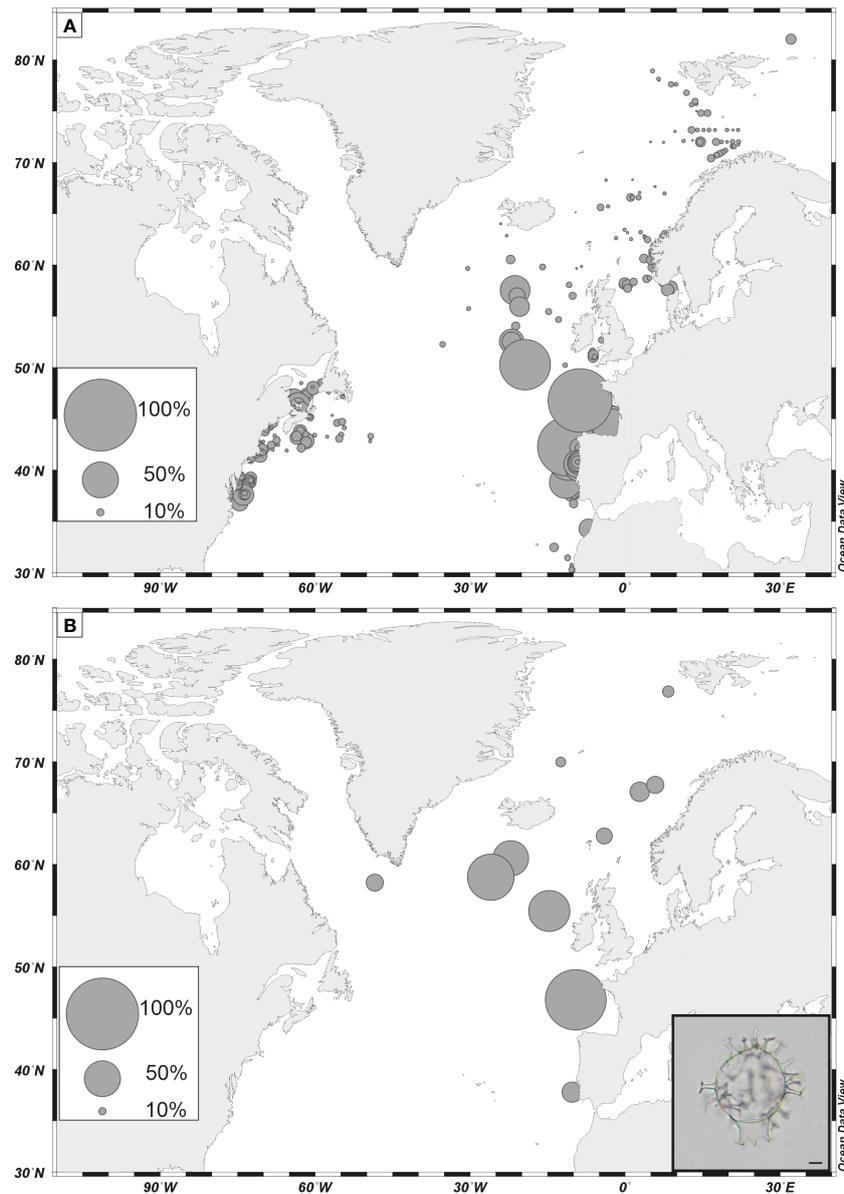

FIGURE 7
Percentages of the main dinocyst taxa in the sedimentary sequence spanning the last 800,000 years at the Ocean Drilling Programme (ODP) 646. Dinoflagellate cysts data are from de Vernal and Mudie (1992) and the isotope stratigraphy from Aksu et al. (1989).

FIGURE 8

(A) Percentages of *Spiniferites mirabilis* in dinoflagellate cyst assemblages of surface sediment as reported in the updated n=1968 database (de Vernal et al., 2020); **(B)** percentages of *Spiniferites mirabilis* in assemblages of the last interglacial (marine isotope 5e). Data are from de Vernal and Hillaire-Marcel (2008), (Van Nieuwenhove et al., 2008, 2011, 2013), Van Nieuwenhove and Bauch (2008), Eynaud (1999), Eynaud et al (Eynaud et al., 2000, 2004), Matthiessen et al. (2001); Penaud et al. (2008). Photos is courtesy of André Rochon, scale bar is 10 μm.

demonstrate the linkages between the assemblages and the parameters to estimate. The standardized database was thus analysed through multivariate techniques such as canonical correspondence analyses (cf. Ter Braak and Smilauer, 1998) to evaluate the strength of the relationships between dinoflagellate cyst assemblages and sea-surface parameters including seasonal temperature, salinity, sea-ice cover and primary productivity. All trials demonstrated that temperature is a determinant parameter but that other parameters are important, including salinity, seasonality and productivity (e.g. Radi and de Vernal, 2008; Bonnet et al., 2010; de Vernal et al., 2013a, 2020; Hohmann et al., 2023). They further show that the strength of the relationship between the assemblage and given parameters may vary

depending on the ocean basin, where the range of different ocean parameters may differ. In the Pacific Ocean, for example, temperature and productivity were revealed to be the most determinant parameters, while in the North Atlantic, temperature and salinity in addition to sea-ice cover explain most of the variance in assemblages (cf. Radi and de Vernal, 2008). On these grounds, different methods of reconstruction were attempted, including the analogue techniques, and calibration techniques such as the artificial neural network and the weighted average partial-least square (Rochon et al., 1999; Peyron and de Vernal, 2001; Bonnet et al., 2010; Hohmann et al., 2023). Validation tests on modern samples have shown good results with all approaches. Low prediction errors could be obtained from the application of
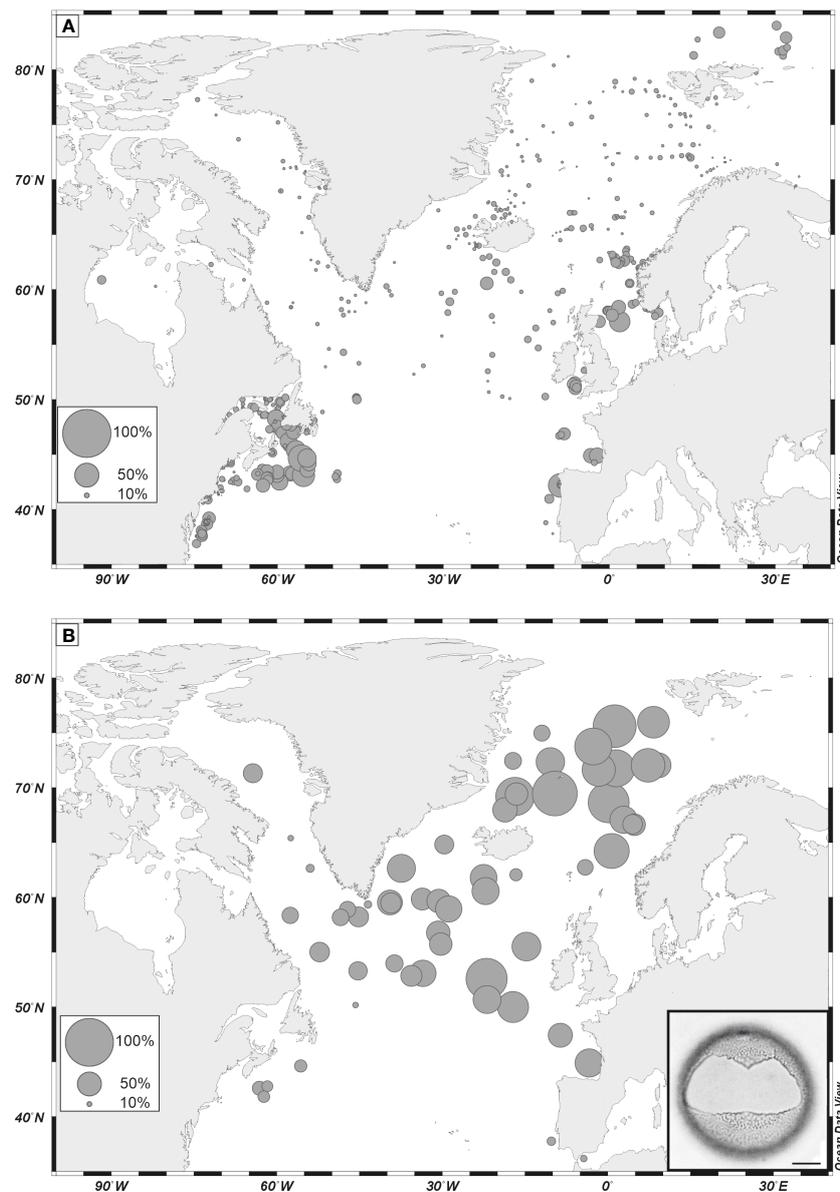
FIGURE 9
(A) Percentages of *Bitectatodinium tepikiense* in dinoflagellate cyst assemblages of surface sediment as reported in the updated n=1968 database (de Vernal et al., 2020); (B) percentages of *Bitectatodinium tepikiense* in assemblages of the Last Glacial Maximum. Data from de Vernal et al. (2005). Scale bar is 10 μm.

calibration techniques on regional data sets. However, when dealing with fossil assemblages, one cannot assume that the modern conditions at the regional scale comprise all past situations. For this reason, the use of modern analogue techniques with databases as large as possible was generally prioritized for palaeo-reconstruction (see Bonnet et al., 2010). Reconstructions from dinoflagellate cyst assemblages in the subpolar North Atlantic have indeed shown extra-regional analogues for late Quaternary samples (e.g. Allan et al., 2018). Moreover, the analogue techniques also identify non-analogue or poor-analogue situations leading to the assessment of the reliability of reconstruction and discarding results when representative analogues are missing.

Three examples of time series illustrating the reconstructions of sea-surface conditions across the North Atlantic cover from the last glacial maximum to the late Holocene are presented here (Figure 11). The example from the Labrador Sea (core HU91–045-094), off southeastern Canada, shows large amplitude changes from glacial to interglacial, with generally dominant heterotrophic taxa and common occurrence of *Islandinium minutum* during glacial time, pointing to seasonal sea-ice cover. The assemblages of the postglacial sediments are dominated by the cosmopolitan phototrophic taxa *Operculodinium centrocarpum* and *Nematosphaeropsis labyrinthus*, and the interval from 11,700 to ~7000 years BP marks the transition with decreasing
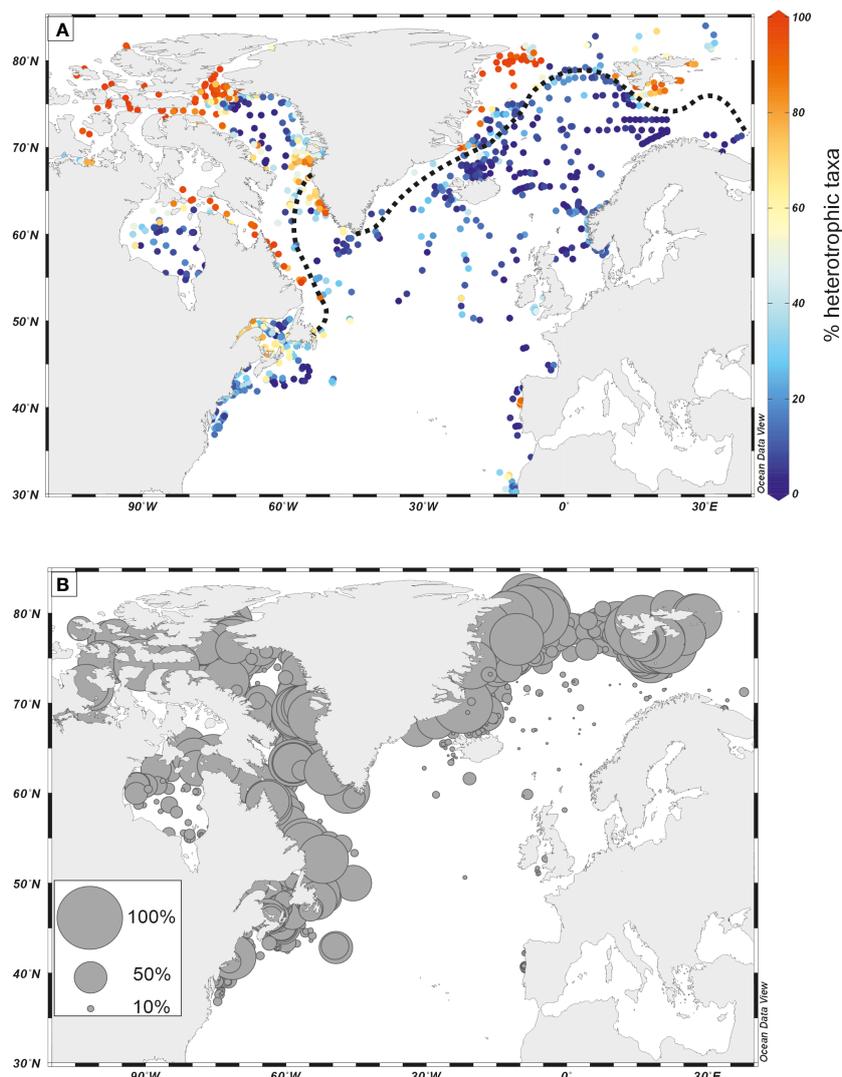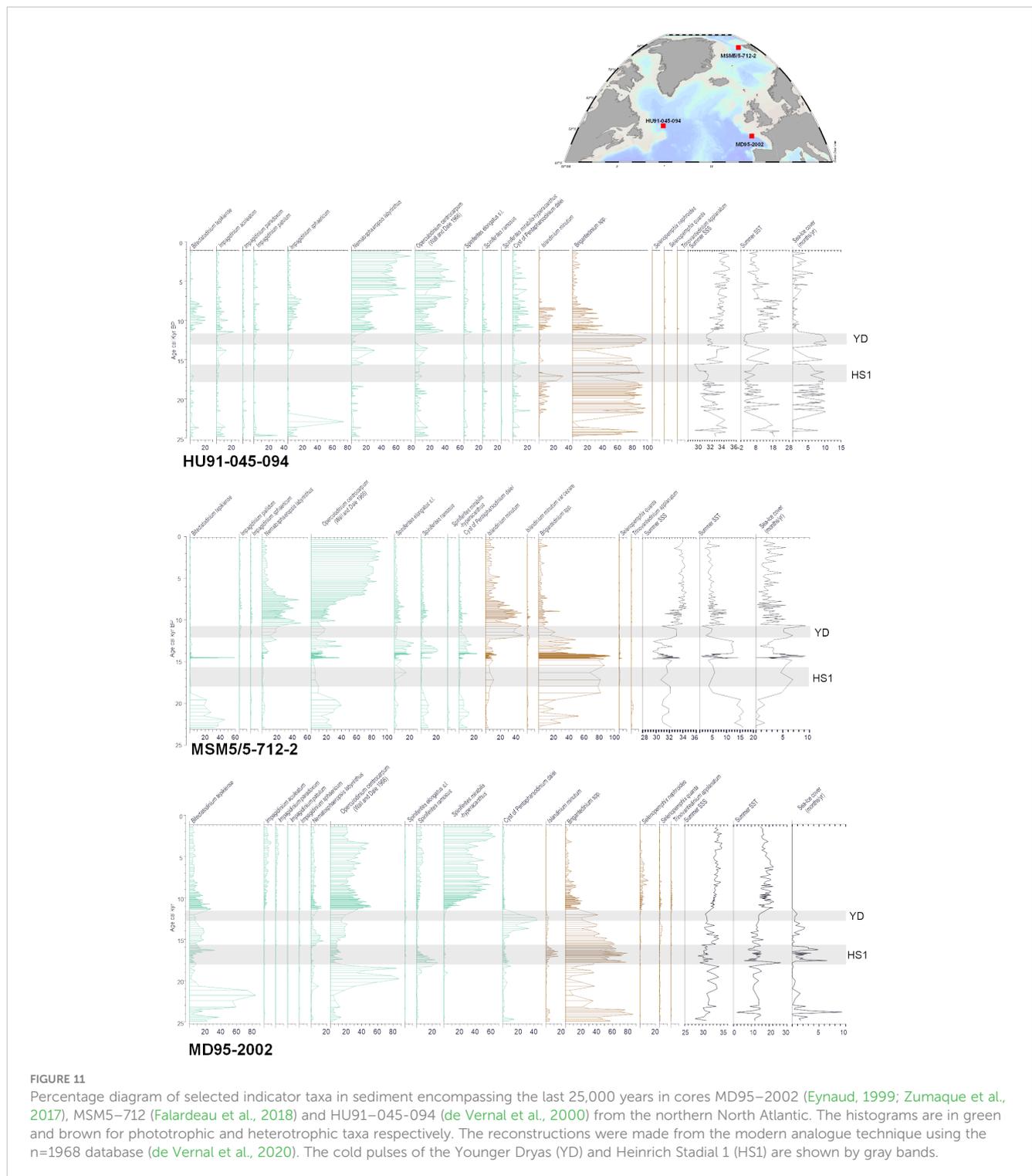
FIGURE 10
(A) Distribution of percentages of heterotrophic taxa in surface sediment assemblages; **(B)** Distribution of percentages of *Islandinium minutum* in surface sediment assemblages. Dinoflagellate cyst data from the updated n=1968 database (de Vernal et al., 2020). Maximum sea-ice (black dotted line) was drawn based on the compiled average position in March (1981–2010) after the National Snow and Ice Data Center (NSDC) online data.

percentages of heterotrophic taxa. It is also characterized by maximum occurrences of *Bitectatodinium tepikiense* and *Impagidinium sphaericum*, thus showing both warm and cold conditions. The reconstructions indicate indeed a large seasonal contrast of temperature with optimum conditions in summer and cold winter in a context of strongly stratified surface waters due to low salinity because of meltwater discharge during ice retreat. The record demonstrates that dinoflagellate cyst assemblages permit to disentangling of winter and summer temperatures, and temperature and salinity. In the example of the core from the Labrador Sea, the simultaneous reconstruction of several ocean parameters is possible because the modern analogues comprise the combination of high-low temperatures under variable salinities in addition to a wide range of seasonal contrasts of temperature (de Vernal et al., 2005, 2020).

In a polar context, the record from the Svalbard margins (core MSM5/5–712-2; Falardeau et al., 2018; Figure 11) in the axis of the

North Atlantic Current flowing northward into the Arctic Ocean illustrates also the transition from glacial to interglacial conditions. The Last Glacial Maximum was characterised by *Bitectatodinium tepikiense* (see Figure 9B) pointing to a warm summer but cold winter, and the Heinrich events were characterised by dominant heterotrophic taxa, leading to reconstructed cold conditions. The transition of the early postglacial, from ~12,000 to 7500 years BP was marked by common *Operculodinium centrocarpum* and *Nematosphaeropsis labyrinthus* and occurrences of both cold water (*Islandinium minutum*) and warm water taxa (*Spiniferites mirabilis*, *Impagidinium sphaericum*), which permitted to reconstructed strong seasonal contrasts of temperatures in a context of low salinity (Falardeau et al., 2018). This example also illustrates large amplitude changes from glacial to interglacial and shows the decoupling of temperatures and salinity.

In a middle latitude context, the data from the western European margins (Core MD95–2002; Eynaud, 1999; Zumaque

FIGURE 11

Percentage diagram of selected indicator taxa in sediment encompassing the last 25,000 years in cores MD95−2002 (Eynaud, 1999; Zumaque et al., 2017), MSM5−712 (Falardeau et al., 2018) and HU91−045−094 (de Vernal et al., 2000) from the northern North Atlantic. The histograms are in green and brown for phototrophic and heterotrophic taxa respectively. The reconstructions were made from the modern analogue technique using the n=1968 database (de Vernal et al., 2020). The cold pulses of the Younger Dryas (YD) and Heinrich Stadial 1 (HS1) are shown by gray bands.

et al., 2017; Figure 11) illustrate high diversity in dinoflagellate cyst assemblages and large changes from glacial to interglacial, but also within the last ice age, which was marked by the succession of dominant heterotrophic taxa and *Bitectatodinium tepikiense* or *Operculodinium centrocarpum*, indicating large variations of salinity and cold pulses with some winter sea-ice cover spreading (Eynaud et al., 2012). At this site, the postglacial interval is marked

by abundant *Spiniferites mirabilis* and *Impagidinium sphaericum* that illustrate warm temperate conditions (Zumaque et al., 2017). The data led to the reconstruction of a mid-Holocene thermal optimum ending around 5000 years BP as at many other North Atlantic sites (Kaufman et al., 2020), but the particularity of the dinoflagellate cyst record is to evidence seasonal contrast, with summer warmth without winter optimum.

5 Palaeo intertropical environments and Southern Hemisphere

Among sea-surface conditions that we reconstruct from biogeochemical proxies and microfossil assemblages, palaeoproductivity may be the most challenging one, besides sea-ice cover. Dinocysts have proved to be good indicators of palaeoproductivity, in particular in regions where net primary productivity is possibly the most dominant control on dinoflagellates (see Radi and de Vernal, 2008; Penaud et al., 2018). Coastal regions, where important river discharges (or plumes) occur, are usually characterized by rich dinocyst assemblages, with a zonation linked to the presence of nutrients and hydrographic conditions. The Atlantic Ocean contains zones where Chlorophyll-a (reflecting the abundance of phytoplankton) is highly abundant, mostly along coastal regions where eastern boundary currents occur (Figure 12A). The West African coastline has several sectors with permanent upwelling systems (Canary Current, Benguela Current). The equatorial region has also upwellings linked to the latitudinal movement of the Intertropical Convergence Zone (ITCZ). In the eastern equatorial Atlantic Ocean, major rivers (Congo, Niger) bring in the marine environment freshwater and nutrients, affecting coastal waters up to a certain distance from the shore. The Congo River discharge is known to create the phenomenon of river-induced upwelling, bringing up to the surface nutrients (e.g., Cadée, 1978; Eisma and Van Bennekom, 1978).

A regional database of dinoflagellate cyst assemblages was reviewed in Hardy et al. (2018), evaluating their potential to reconstruct sea-surface conditions, in particular past productivity. Of the 237 sites that were selected, 164 were retained as they could be related to pre-industrial conditions for productivity (using Vertically Generalised Production Model, VGPM) and SST. In this study, two NPP models were used, the VGPM and the Eppley-VGPM ones, where the Eppley-VGPM tends to give higher NPP values when SSTs are high. The statistical analysis (CCA) performed on these 164 assemblages (Figure 12B) shows a clustering of assemblages that more or less identifies the different regimes of oceanographical conditions. A canonical correspondence analysis carried out on the taxa occurring in the 164 assemblages shows that taxa are ordinated along three dominant directions (Figure 12C), which strongly suggests that the species are predominantly controlled by SST and productivity, even though the two NPP vectors have a different direction. Taxa in the upper right quarter are usually found in open ocean and western boundary current systems. Taxa in the bottom left quarter usually respond to warmer temperatures compared to the taxa in the bottom right quarter. Most of the heterotrophic taxa are ordinated closely to both NPP vectors.

This situation is similar back in time. Despite rare organic-walled dinoflagellate cyst records in this region, contrasting data highlight the complex response of dinoflagellate cysts to environmental changes. Selected records covering the last 25,000 years, with robust age models, show that the eastern side of the tropical Atlantic Ocean was mostly dominated by heterotrophic taxa, notably *Brigantedinium* spp., during the last glaciation, and that the Holocene is characterised by a dominance of phototrophic taxa, mainly *O. centrocarpum* and some *Spiniferites* species (Figure 13). Heterotrophic taxa also captured the latitudinal migration of the ITCZ, in particular near the deltas of large rivers (e.g., Marret et al., 2013; Hardy et al., 2018). In the western side of the tropical Atlantic Ocean, the records show the dominance of phototrophic taxa, essentially *O. centrocarpum*, with very little change between glacial and interglacial conditions.

Further south, very few Quaternary records are available, but they all show a dominance of heterotrophic taxa during glacial marine isotopic stages, notably the MIS2; they also have demonstrated strong potential to trace latitudinal movements of the different fronts (e.g., Esper and Zonneveld, 2007). Off the southwest African coast, ODP Site 1087 integrates signal of Agulhas leakages over the last 500,000 years based on biogeochemical and microfossil proxies; dinoflagellate cysts were used to reconstruct sea-surface temperature, showing a good agreement with alkenone-based SSTs (Petrick et al., 2015). These few studies provide evidence that dinoflagellate cysts can be used to reconstruct complex oceanographic changes over the Quaternary.

6 Environmental issues and dinoflagellates

Some dinoflagellates are notoriously known for lethal toxin production (e.g., *Alexandrium* sp.); others are red-tide producers, and while not being lethal, can severely affect aquatic ecosystems through the process of eutrophication (e.g., Anderson, 2019). Global monitoring shows that most coastal regions are now affected by HABs (either red tide or toxicity, or both) (https://data.hais.ioc-unesco.org/); that was not the case half a century ago where fewer events were reported or recorded. Causes of such widespread phenomenon are, among others, related to increased agricultural activities, with the release of nutrients (N and P), favouring algal blooms. Transport of organisms in ship ballast waters has also been a contributor. Recent studies have been linking changes in climatic conditions to phytoplankton communities (e.g., Hinners et al., 2019). Therefore, it was very tempting to trace back in time the occurrence of species related to eutrophication to better understand the mechanisms behind their distribution. The Gulf of Mexico is an exemplary case study where the clear relationship between the abundance of specific cyst taxa (mostly heterotrophic species) and nutrient enrichments due to the use of agricultural fertiliser has been established (Price et al., 2018). Of the known species producing toxins or red-tides, very few produce a cyst that can preserve well in sediments (see Table 1, thecate species in bold). Cysts of *Alexandrium* sp. are often observed in recent sediments and up to a few hundred years but do not seem to be preserved beyond that (e.g., Head et al., 2006). It was debated that these cysts may have been confused with the ones produced by the calcareous dinoflagellate species, *Scrippsiella trifida*. Mudie et al. (2002) reported sporadic presence of
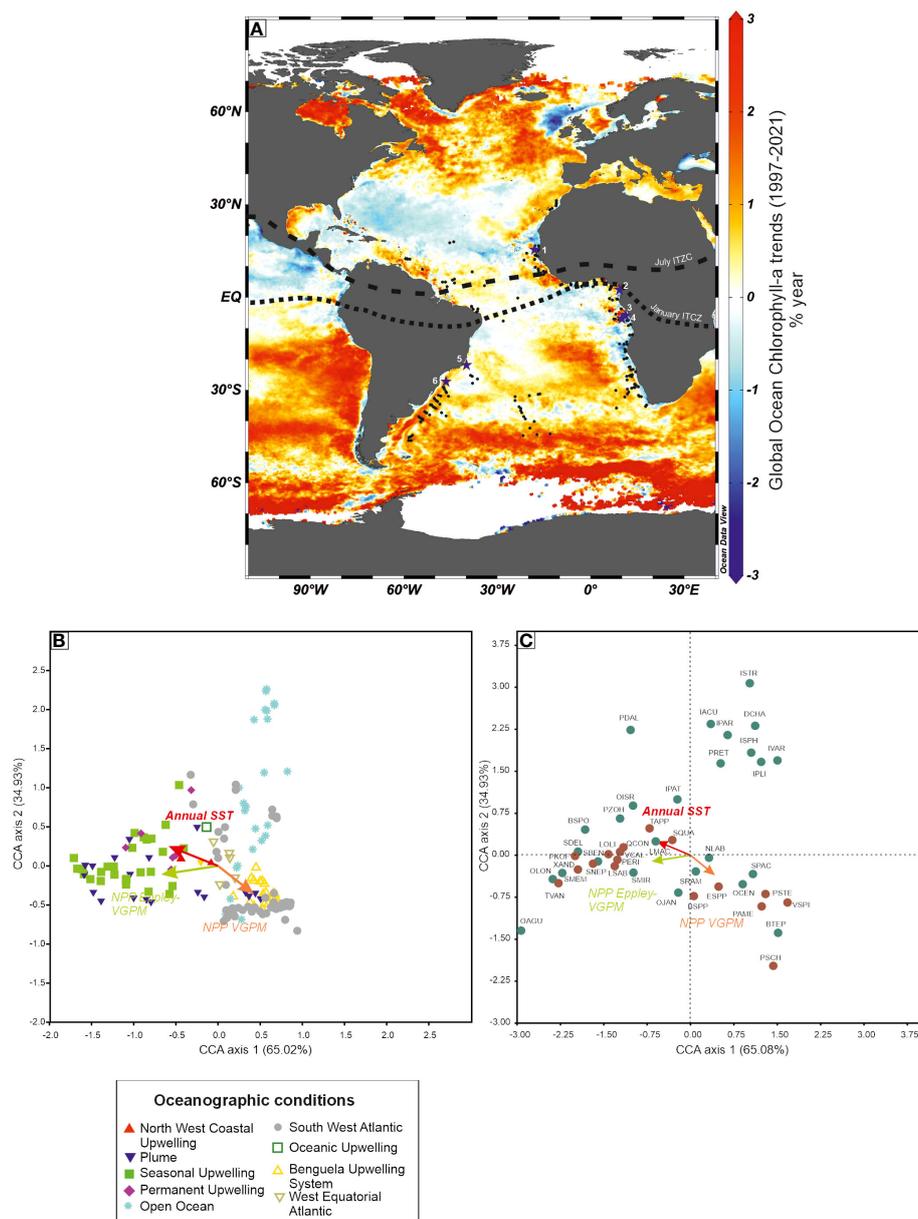
FIGURE 12

(A) Global distribution of ocean Chlorophyll-a (change in mass concentration over time) (DOI (product): https://doi.org/10.48670/moi-00230); location of dinoflagellate cyst assemblages in surface sediments (from Hardy et al., 2018); position of the Intertropical Convergence Zone; location of cores cited in the text and Figure 13 [1: core GeoB9508−5 (Bouimetarhan et al., 2013); 2: core GeoB4905−4 (Marret et al., 2013); 3: core KZAI-01 (Hardy et al., 2016); 4: Core GeoB1008−3 (Dupont et al., 1999); 5: Core GeoB3202−1 (Gu et al., 2020); 6: Core GeoB2107−3 (Gu et al., 2017)]. **(B)** Canonical correspondence analysis on the 164 assemblages from Hardy et al. (2018) with position of the controlling factors (Annual Sea-Surface Salinity, Annual Sea-Surface Temperature and Net Primary Productivity (NPP) (see Hardy et al., 2018). Symbols are allocated to assemblages in relation to the oceanographic conditions at their location. **(C)** Canonical correspondence analysis on the taxa occurring in the 164 assemblages, with phototrophic taxa in green and heterotrophic taxa in brown (adapted from Hardy et al., 2018), and delimited by four quarters by dotted lines. Variances in % are indicated between brackets. CCA was run on percentage data of the 164 assemblages.

Alexandrium cysts off Newfoundland during the Holocene period, their abundance linked to warming SST. However, Head et al. (2006) demonstrated that these cysts were produced by *S. trifida*. Nevertheless, other species, which produced resistant cysts, have shown high abundance during warm episodes (*L. machaerophorum* during the Holocene in the NW Atlantic Ocean, Mudie et al. (2002); *Polysphaeridium zoharyi* during the Middle Eocene Climatic

Optimum warming in east equatorial Atlantic, Cramwinckel et al., 2019).

Fjords have been particularly scrutinised, due to their propensity of becoming eutrophic in recent times. Dale et al. (1999) introduced the concept of using abundance of dinoflagellate cysts as "indicators of cultural eutrophication". *L. machaerophorum*, a species occurring worldwide, with a large tolerance to salinity and temperature, has
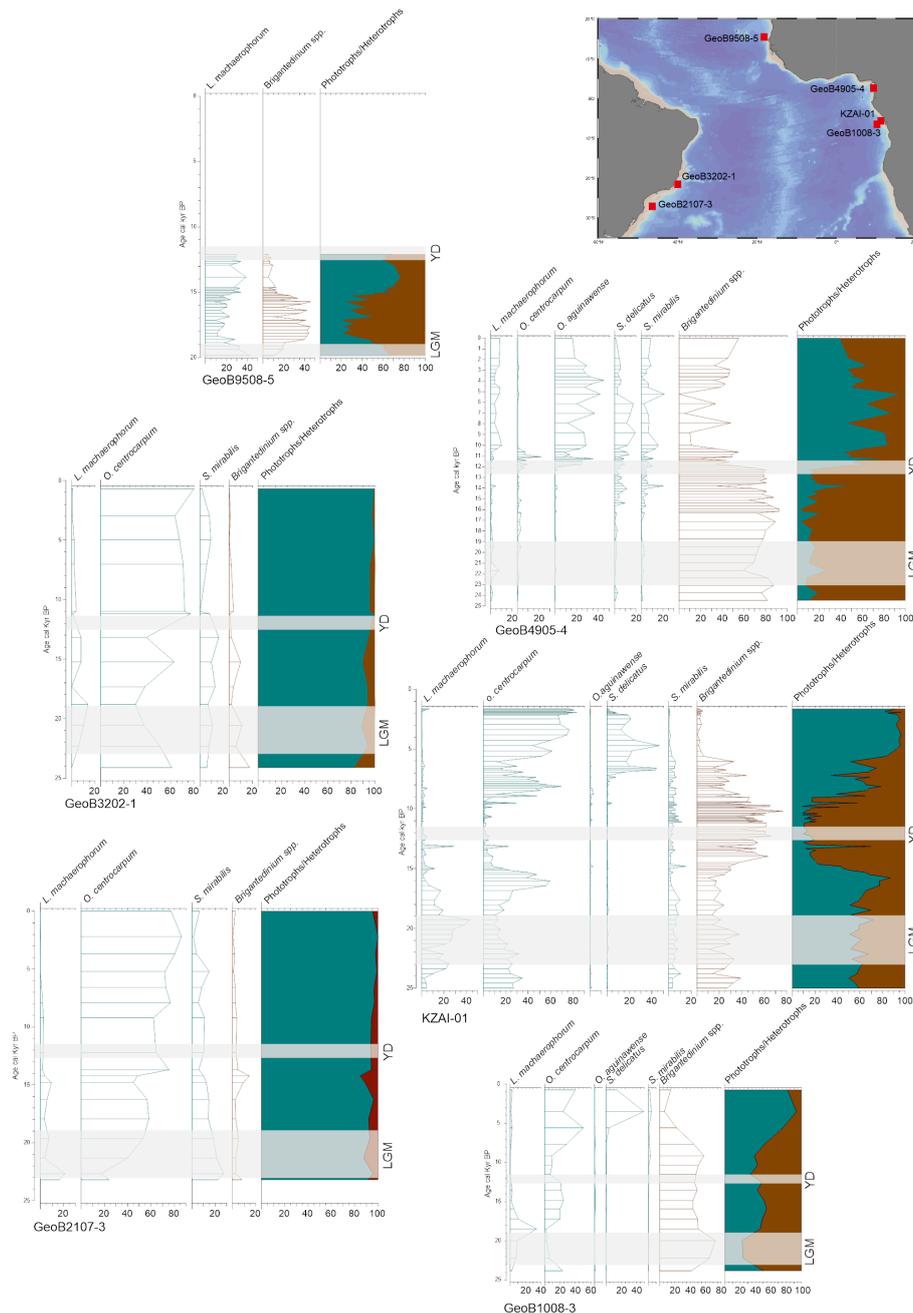
FIGURE 13
Selected cores in the tropical regions of the Atlantic Ocean, covering the last 25,000 years, with percentages of dominant dinoflagellate cysts (see caption in Figure 12 for details about cores). LGM, Last Glacial Maximum; YD, Younger Dryas.

seen their abundance largely increase when additional nutrients entered the waters of the inner basin of the studied fjord (Oslofjord, Norway). Not far from this site, another record from Gullmar Fjord (Sweden) highlights a more complex story, with no strong evidence of the abundance of *L. machaerophorum* being related to nutrient enrichments (Harland et al., 2006).

Our increasing knowledge of the ecology of dinoflagellate cyst species and their biogeographical distribution highlights that their past occurrence reflects a complex history of oceanographic changes, in particular for more recent times where human

activities had a profound impact on coastal ecosystems. However, it is possible to use past assemblages during interglacial periods to obtain an insight into environmental conditions in a warmer world.

7 Closing remarks and perspectives

Compared to other microfossils, dinoflagellate cysts are very particular palaeoecological-palaeoceanographical indicators as summarized in a few points below.

(1) They are organic-walled biogenic indicators of productivity in the photic zone that are usually well preserved in marine sediments unlike those formed of opal silica and calcium carbonate, such as diatoms and coccoliths respectively, that may dissolve when there is undersaturation of silica and carbonate in the water column. From this viewpoint, dinoflagellate cysts are useful and complementary proxies of primary productivity, providing there is no oxidation of organic matter.

(2) The fossilisable cysts of dinoflagellates are mostly abundant in neritic areas and along continental margins and rare in distal offshore settings, possibly because they constitute the benthic stage of hypnozygotes with only a few taxa having the ability for dispersal over long distances in surface waters of the deep ocean. Among those, *Impagidinium* species stand out in addition to the cosmopolitan taxa *Operculodinium centrocarpum* and *Nematosphaeropsis labyrinthus*.

(3) Dinoflagellates include taxa with a wide range of trophic behaviors, phototrophic, heterotrophic and mixotrophic, notably. While phototrophic taxa usually dominate in oceanic settings, heterotrophic ones are often abundant in nearshore areas, and also along the sea-ice edges and the upwelling zones, where diatom blooms dominate the primary production and sustain the development of heterotrophic dinoflagellates. Hence, dinoflagellate cysts offer a holistic view of productivity, beyond what is strictly related to primary production.

(4) Cyst-forming dinoflagellate occur from the equator to the Arctic and Antarctic, where they form assemblages typical of sea-ice environments, often dominated by heterotrophic taxa. Hence, they are useful for making inferences about sea-surface temperature, from tropical to freezing.

(5) Dinoflagellate cyst assemblages with different taxonomical compositions encompass low to high-salinity environments, from estuaries to open oceans, which make them one of the rare proxies of salinity. Similarly, because salinity is closely tied to stratification and thermal inertia making large seasonal contrasts at high latitudes, dinoflagellate cysts also appear to be one of the rare indicators of seasonality.

For all the reasons mentioned above, dinoflagellate cyst assemblages are unique proxies allowing the documenting of past climate and ocean conditions with regard not only to temperature but also considering seasonality, salinity, sea-ice cover, and productivity. However, the taxonomy of dinoflagellate cysts is not necessarily easy, especially when considering the polymorphism of some taxa and the existence of cryptic species. Moreover, the processing of the sediment before microscope observation and the analyses of the dinoflagellate cyst population are time-consuming. As a consequence, the scientific community is currently exploring techniques such as those based on molecular biomarkers and ancient DNA that are less tedious than micropalaeontology to document past dinoflagellate populations and/or species as proxies for key environmental parameters.

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Conflict of interest

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